

An Experimental Analysis of the Escape Response of the Gastropod *Strombus maculatus*¹

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ABSTRACT: The escape response of *Strombus maculatus* is described in detail, including the apparent adaptive morphology of the foot, operculum, and eyestalks. The response is elicited by a chemical stimulus from two molluscivorous species of *Conus* and two gastropod-eating species of *Cymatium* but not from other predatory species of these genera. *Strombus* habituated within three trials to a solution of "factor" from *Conus pennaceus*, but habituated only rarely, and then only after many trials, to contact with the live *Conus*. It was concluded that the eyes of *S. maculatus* are not used to see the *Conus*; however, eye removal significantly disrupted the orientation of the escape response, suggesting that the animal monitors some environmental cue such as polarized light. Tentacle removal appeared to interfere with escape response orientation but only to a variable extent.

HERBIVOROUS GASTROPODS exhibit distinctive escape behavior from sea stars (Bauer 1913, Feder and Christensen 1966) and predatory gastropods (reviews by Kohn 1961, Robertson 1961, Kohn and Waters 1966, Gonor 1965, 1966). *Strombus* has the remarkable ability to escape from predators by rapid lunges, using the operculum to push against the substrate (Kohn and Waters 1966). Gonor (1966: 227) described the response of *S. gibberulus* and *S. lubuanus* to *Aulica vespertilio* and *Conus marmoreus*. Both species of *Strombus* escaped by "moving away with quick kicks of the foot until they were about 30 cm away". Kohn and Waters (1966) analyzed quantitatively the escape response of *S. canarium* to *C. textile*: the animal "leaped" approximately 16 mm every 1.6 sec, at a mean rate of progression of 6.8 mm/sec. In these species of *Strombus*, escape behavior differs from normal locomotion only in its much accelerated pace. Normal locomotion has been described by Parker (1922) as "leaping," in which the

posterior end of the foot is thrust against the substrate, causing the shell and head to lunge forward. Little additional work has been done on strombid locomotion, and as Kohn and Waters (1966: 341) indicated, "the component steps of the process have not been analyzed and the functional morphology remains to be studied in detail." Recently Berg (1972) described the ontogeny of several strombid behavioral patterns, including locomotion. In addition, Berg (1974) made a subsequent analysis, based on the present report, of behavior patterns in 10 species of Indo-Pacific strombid gastropods.

I studied escape behavior of the Hawaiian species *Strombus maculatus* Sowerby, which reacts to the presence of gastropod predators, particularly *Conus pennaceus*. This response differs from those described previously for *Strombus* in that *S. maculatus* actually propels itself backward, clear of the substrate, traveling up to 2.5 times its shell length, activity never observed during normal locomotion (described briefly below).

This paper describes the escape response in precise terms and discusses the associated adaptive morphology. Locomotory rates were analyzed cinematographically for comparison with Kohn's work. Experimental studies investigated: (1) the nature of the stimulus and conditions

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that elicit the response, (2) the attenuation of the response to repeated stimuli, and (3) the means by which *Strombus* receives the stimulus and orients the response during escape from *C. pennaceus*. The attenuation of a gastropod escape response was studied briefly by Margolin (1964). He found, as did Feder (1948, cited in Bullock 1953) and Feder (1963), that the response eventually ceases after the animal has been "sensitized" to the stimuli.

METHODS

The 12 *Strombus maculatus* used in this study (size range 1.7–3.4 cm) were collected on sand and algae-covered intertidal benches around Oahu, Hawaii. Six were fully grown and six were subadults (outer lip of shell not yet thickened). The animals were maintained in a shaded outdoor seawater table with a sand bottom and fresh, circulated, unaerated seawater. Habituation experiments were carried out in a similar seawater table (67 × 94 cm). Motion pictures were made at 16 frames per sec with a Bolex H-16 camera (16 mm).

Conus and other reef-dwelling molluscivorous gastropods were tested by being placed near *Strombus*. Parts of *Conus pennaceus* and the water in which the predator had been living were introduced to see whether they would elicit the escape response.

Two types of experiments concerned attenuation of escape: a *Strombus* was stimulated every 5 min by (1) contact with a live *C. pennaceus*, and (2) by 20 cc of seawater containing a chemical factor produced by *C. pennaceus* (hereafter referred to as "*Conus* factor"). A "standard" factor solution was obtained by allowing three to four *C. pennaceus* to remain in 1 liter of unaerated seawater at ambient temperature for 2 hr. In both sets of experiments, the response was recorded in terms of latency and numbers of jumps following each stimulus presentation.

I studied the orientation of the response by making eyestalk and tentacle ablations on animals that had been narcotized in 7.5 percent $MgCl_2$ diluted 2:1 with seawater. On the day following an operation, at which time the operated animals appeared normal and responsive, experiments were conducted in seawater in a shallow tray, 1 m² in area and 8 cm deep. Sand

was attached to the bottom with a coat of resin, and concentric circles, 2.5 cm apart, were marked on the sand and numbered from the center outward. A *Strombus* was placed in the center circle, and escape was elicited by holding a live *Conus* next to it. The number of the circle in which the animal landed after each jump was dictated into a tape recorder. Sixty-five escape sequences were analyzed from three animals.

RESULTS

Description of Response

Normal feeding of *Strombus maculatus* consists of slow ciliary gliding with periodic shifting of the shell forward (in contrast to Parker's (1922) description of "leaping") while the proboscis works back and forth, grazing on minute algae on the substrate. When *Conus pennaceus* is detected within 5 to 10 cm, *Strombus* stops both locomotion and feeding and partially withdraws into, and lowers, the shell. The eyestalk tentacles, which normally extend forward and wave in small arcs, are directed toward the *Conus* and increase their rate of waving, as judged subjectively. The onset of escape is triggered usually either by some movement of the *Conus* or by direct contact. The *Strombus* then pushes quickly against the substrate with the posterior part of the foot, propelling itself backward and slightly to the left. This small initial movement causes the aperture to face upward or to the side after the animal has landed. The foot then flexes forward and down, its posterior tip flattened against the operculum, which is dug into the substrate beneath the shell (Figure 1A2). Next, the foot violently straightens, causing a backward flight above the substrate for several centimeters (Figure 1A3–A7). During the entire response, the proboscis and eyestalks are extended. The sequence of Figure 1A is repeated until the animal has removed itself from the *Conus*. After the final jump, the animal rapidly swings the proboscis back and forth across the substrate, secures a grip with the foot, shifts the shell dorsad, and moves with its normal pedal locomotion, testing the environment with the proboscis. At this point the animal either burrows into the sand or glides away.

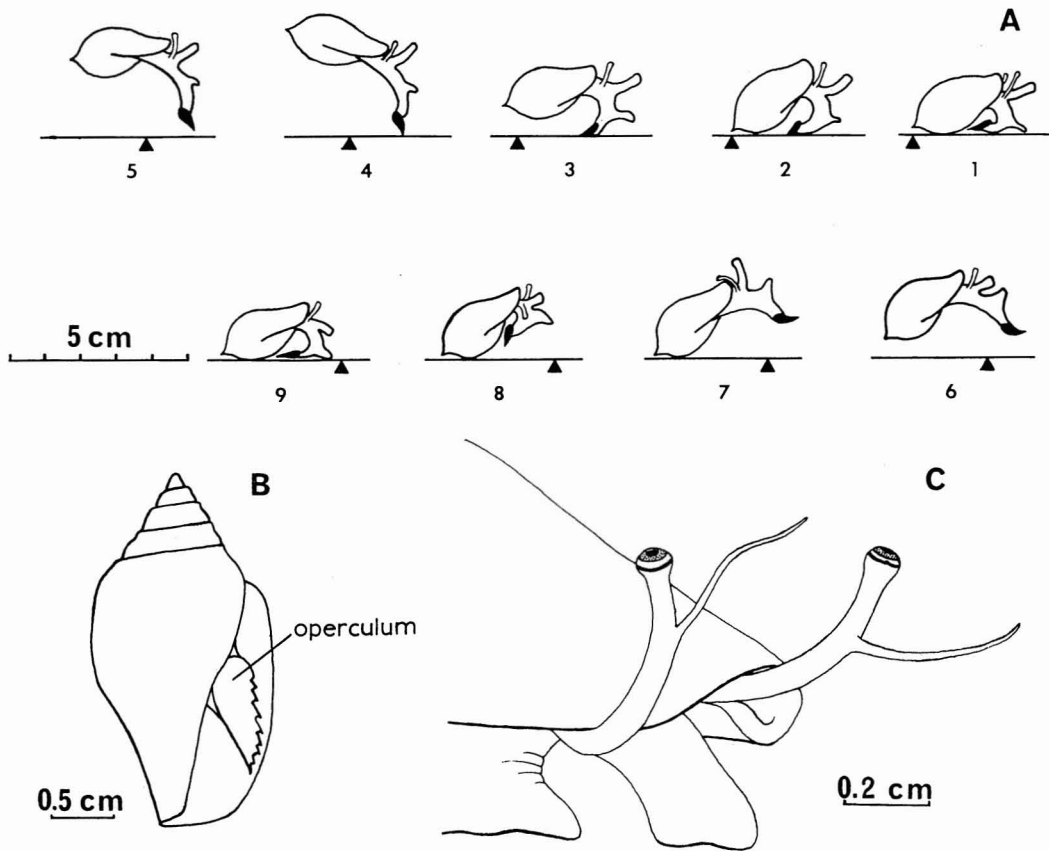


FIGURE 1. *A*, An escape jump of *Strombus maculatus*, drawn from consecutive motion picture frames; note use of operculum. *B*, View of *S. maculatus* withdrawn into the shell, exposing only the operculum. This illustrates the operculum's serrated edge and small size as compared to the length of the aperture and shell. *C*, Eyestalks and tentacles of *S. maculatus*, shown during feeding. The extended proboscis and anterior end of the foot are also seen protruding from the shell. The tentacles may be withdrawn or extended beyond the length illustrated.

Escape varied among individuals and from day to day in a single individual. Jumps varied from 2–63 per sequence, with an average ($N = 25$) for a *Strombus* 2.9 cm in length of 19 (range 5–36). This agrees well with a mean value of 18 jumps per response ($N = 16$) subsequently recorded by Berg (1974) for the same species. On one occasion a *Strombus* did not jump but instead glided away from a *Conus*.

Functional Morphology

The operculum of *Strombus maculatus* is highly modified to form a hard, pointed pivot from which the animal can gain leverage to launch itself (Figure 1*A–B*). It is attached to an epipodial flap on the posterodorsal part of the

foot and is serrated along its right edge. The serrations seem to grip the substrate efficiently as the animal jumps, instead of creating a cutting edge for a defensive weapon, as suggested by Charles (1966). The operculum appears more important for its use in the escape response than for its typical function in other gastropods (closing of the aperture), for the animal rarely withdraws into its shell as a protective reaction; instead, it usually makes the escape response. Only the most intense stimuli (e.g., continuous prodding with a pin) cause the snail to cease the escape response and withdraw into the shell.

The foot of strombids is striking in several respects. Its sole is much narrower than that of most prosobranchs, and only the anterior third is used for adhesion (Abbott 1960). In *S. maculatus*,

the elongate, muscular portion, extending through the aperture, is quite narrow, allowing the animal spectacular agility in reaching out and positioning the operculum. Through this precise placement of the operculum, the animal is able to direct its backward jump and also to right itself with a quick foot extension and kick against the substrate.

Another series of adaptations is seen in the structure of the well-developed eyestalks (Figure 1C). The eyes themselves are large and extend well to the sides of the body in a position where they are suitably placed to detect objects, including predators, in the environment. The long, mobile, presumably chemosensitive tentacles would, by virtue of their considerable separation, provide the animal with a maximal chance to detect a chemical gradient around it. Well-developed tentacles are lacking in species of *Strombus* that do not move by rapid jumps (Charles 1966).

Nature of the Stimulus

Preliminary observations indicated that *Strombus maculatus* perceives *Conus pennaceus* not only by contact but also chemically (at least up to a distance of about 5 cm), as Kohn and Waters (1966) have suggested for *S. canarium*. *Conus marmoreus*, which is molluscivorous, also elicited the response, whereas *C. rattus*, *C. ebraeus*, *C. flavidus*, and *C. chaldaeus*, all vermivorous, did not. Similarly *Cymatium nicobaricum* and *Cymatium gemmatum*, both gastropod-eaters, elicited the response, whereas *Cymatium pileare*, a bivalve-eater (J. R. Houbbrick, personal communication) did not.

The empty shell of *Conus pennaceus* (with periostracum) occasionally elicited escape. *Conus mucus* had no effect when pipetted as a homogenate in seawater, but it caused a strong response when swabbed on *Strombus* skin with a pipe cleaner. That *C. pennaceus* releases a factor into the water was shown in pilot experiments in which individuals were retained in seawater

for 1–25 hr, and then this water was pipetted at *Strombus*. This did not always release the response, although the *Strombus* invariably lowered its shell and stopped feeding. The *Conus* factor solution was less effective if the period exceeded 18 hr.

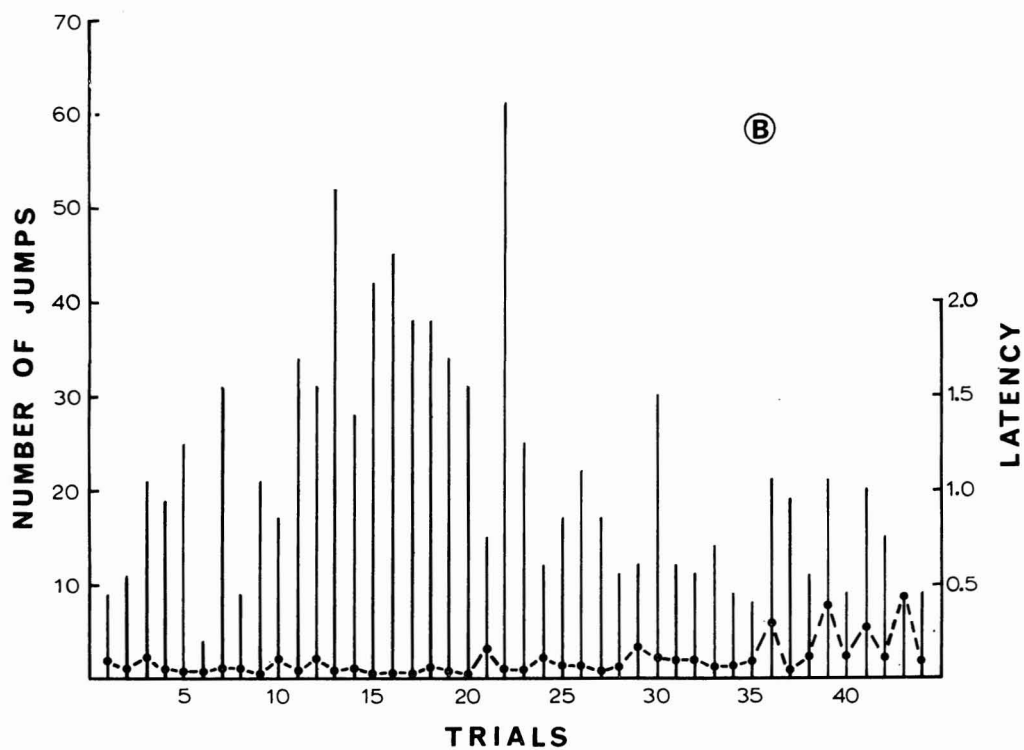
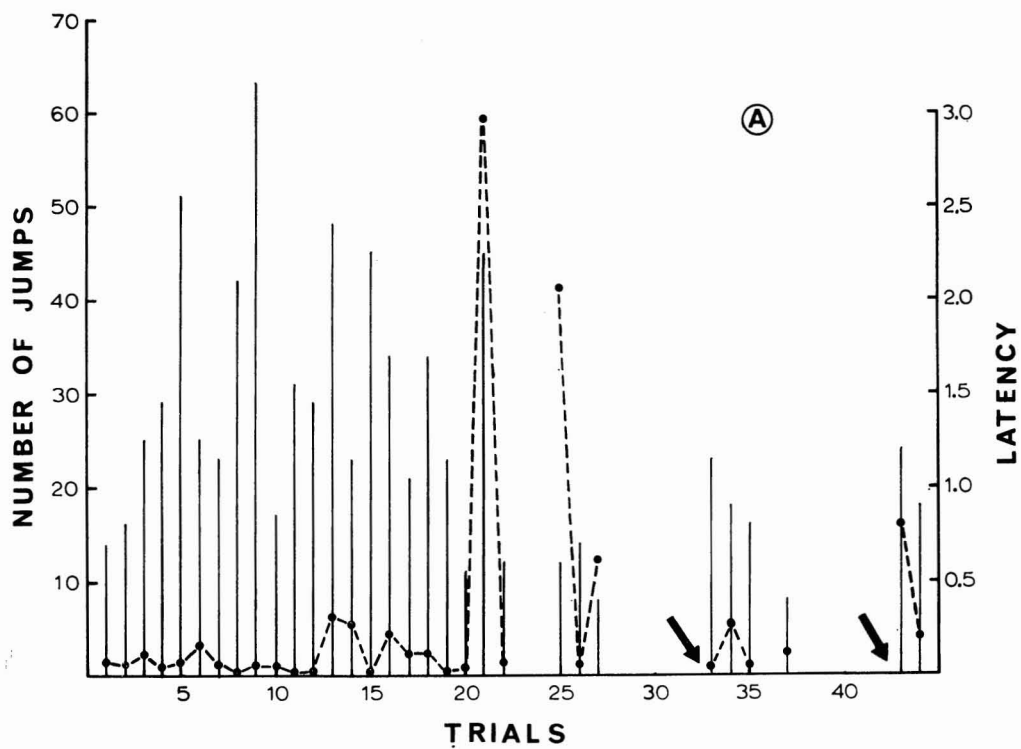
Locomotory Rates

Cinematographic sequences of locomotion showed that, while feeding, the animal's speed varied between 0.4 mm/sec and 1.5 mm/sec (mean rate 1.0 mm/sec). This compares with a mean rate of 0.18 mm/sec (measured by Berg 1974) for *Strombus maculatus* of similar size. During the escape response, the animals' speed increased from 36 to 57 mm/sec (mean rate 46.4 mm/sec) and locomotion was accomplished only by the backward "jumping" (used hereafter to describe escape locomotion) shown in Figure 1A. Berg (1974) measured a mean escape rate of 15.7 mm/sec in his analysis of *S. maculatus*. In contrast with the data reported by Kohn and Waters (1966) for *S. canarium*, in which the leap distance remained constant while the interval between leaps decreased, the data for *S. maculatus* show that both variables changed. The mean distance between jumps in the present study increased from 12 mm during feeding to 37 mm during escape. The mean interval decreased from 8.2 sec (feeding) to 0.8 sec (escaping). The maximum speed of 57 mm/sec exceeds those rates reported by Kohn and Waters (1966) by nearly fivefold and that of Berg (1974) by nearly threefold.

Attenuation of the Response

LIVE *Conus* AS A CONTACT STIMULUS: I elicited escape responses from four *Strombus* by causing contact with a live *Conus* every 5 min. Before each experiment a *Strombus* was placed on the sand bottom of a shaded outdoor seawater table and was left undisturbed for 5 min. Then for each trial a *C. pennaceus* was held close to the *Strombus*

FIGURE 2. Response of *Strombus maculatus* to repeated contact exposures to live *Conus pennaceus*. Solid lines indicate number of jumps; dashed lines with solid circles indicate latency of the response, in minutes. Each graph represents the activity of only one animal. A, Experiment in which complete cessation occurred and response returned only after needle prods (arrows). Absence of a vertical line (e.g., trials 23 and 24) indicates no response after 3 min of continuous stimulation. B, A more typical experiment, showing gradual attenuation of the response and erratic increase in latency.



until the molluscivore extended its siphon and touched the snail's eyestalks. When jumping occurred the *Conus* was placed (inverted) on the sand where it remained until the *Strombus* completed its response (which lasted usually less than 3 min). The four *Strombus* underwent 12, 24, 44, and 44 trials, respectively.

Three animals showed attenuation of the response (an average decrease in the number of jumps per trial) with repeated stimulation. An example is shown in Figure 2B. The fourth showed two cycles of alternating decrease then increase in response intensity during the 24-trial experiment. Only one animal showed complete cessation of the response (Figure 2A), which occurred after 22 trials. In this experiment, the response returned at trial 25 but with a very long latency (2 min). Then the response faded and disappeared within the next three trials and did not return during the following five trials. At this time the animal was gently prodded with a needle until it withdrew entirely into its shell. On the next trial the escape response returned and lasted for several more trials, after which it again disappeared. Following another interval of five trials and a further needle-prod stimulus, the response returned.

In general, response latencies (dashed lines, Figure 2) remained low initially, then increased and became more erratic with time. Recovery of the normal response occurred after 24 hr in these animals.

EXPERIMENTS WITH THE *Conus* FACTOR: The above experimental format was used with six other *Strombus maculatus* (12–17 trials per experiment) but with the *Conus pennaceus* factor as a stimulus. The stimulus solution (20 cc) was delivered at an average rate of 0.7 cc/sec (measured in three experiments) through a glass capillary that had been drawn to a tip-diameter of 0.5 mm and was held 5 cm from the anterior end of the *Strombus*. Since not all individuals reacted to the stimulus, several were tested before each experiment until one gave a positive response. This animal then would be selected for the experiment. In all experiments, the response attenuated completely after a maximum of three trials. Immediately after the 10th trial, in all six experiments, the animal was prodded with a needle until it withdrew completely into

its shell. In two experiments, the response returned after the needle prod. In one, the *Strombus* made four jumps after having been prodded with the needle, but not after subsequent presentation of the *Conus* factor.

Strombus also makes a typical escape response when placed on a dry surface. I ended each *Conus* factor experiment by placing the animal on a dry wooden platform. All animals so tested produced the response, thus eliminating the possibility that complete attenuation of the response was due to muscular fatigue.

Orientation of the Response

The shallow seawater tray with concentric numbered circles on the sand bottom was used in these experiments. The aims of this study were to determine whether *Strombus* orients its escape response away from the locus where it encounters a *Conus* and to discover which sense organs might be involved in such orientation. I made specific ablations to obtain this information.

A series of escape response paths was averaged and plotted for an intact *Strombus* (Figure 3). This experiment was designed to test whether the *Strombus* visually oriented away from the *Conus*. Therefore, the *Conus* was either allowed to remain in the center circle of the tray during the course of each *Strombus* escape response (Figure 3A) or was removed as soon as the *Strombus* had begun its escape response (Figure 3B). To check these results, I removed the eyes of the same *Strombus* and conducted another series of tests (Figure 4A). Finally, to interfere with possible chemosensory orientation, I removed the tentacles of the same animal and conducted a third series of tests (Figure 4B). In these tests, the differences in escape paths before and after the operations became apparent only after the animal had made the first five or so jumps. I used two other animals in orientation experiments to provide data similar to those shown in Figures 3 and 4. I removed only the left eyestalk and tentacle of one of these snails to see whether the escape pathway would become disrupted (perhaps circular).

Table 1 summarizes the results of these experiments. Chi-square tests on these results are shown in Table 2 and indicate that the most

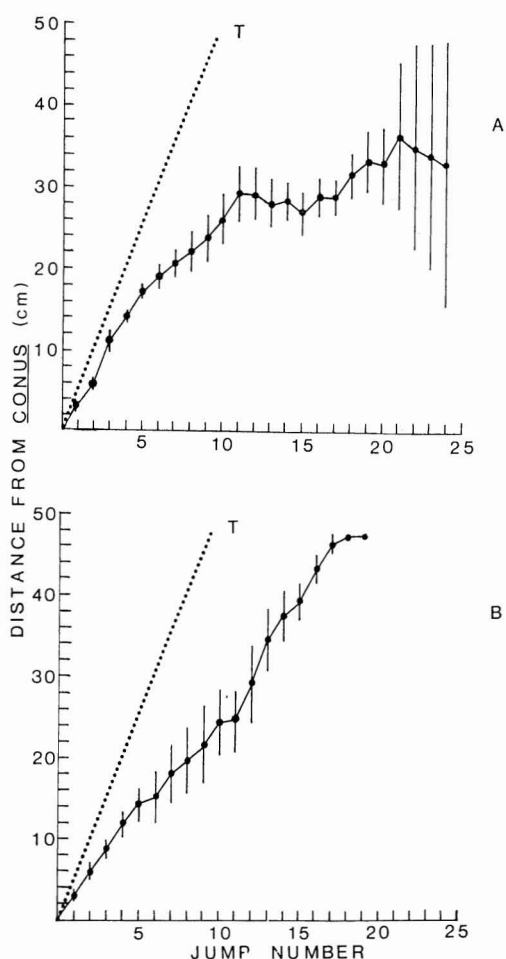


FIGURE 3. Escape paths plotted for an intact *Strombus maculatus*. The number of the circle in which the animal landed, beginning with the center circle, was plotted against sequential jump number. Each graph shows averaged replicates for one animal, indicating the variation (mean \pm standard error) observed for that individual. The dotted line, T, indicates the theoretical path of maximum efficiency. See Methods for description of experiment. A, *Conus pennaceus* remained present following contact stimulation ($N = 9$). B, *Conus* absent (removed) following stimulation ($N = 8$).

effective disruption of the escape path was produced by the blinding operation ($0.001 < P < 0.01$). Removal of tentacles after blinding did not produce a much greater disruption ($0.05 < P < 0.10$); therefore, when both eyes and tentacles were removed together, the major contribution to the significant disruption ($P < 0.001$) probably was due to blinding. One

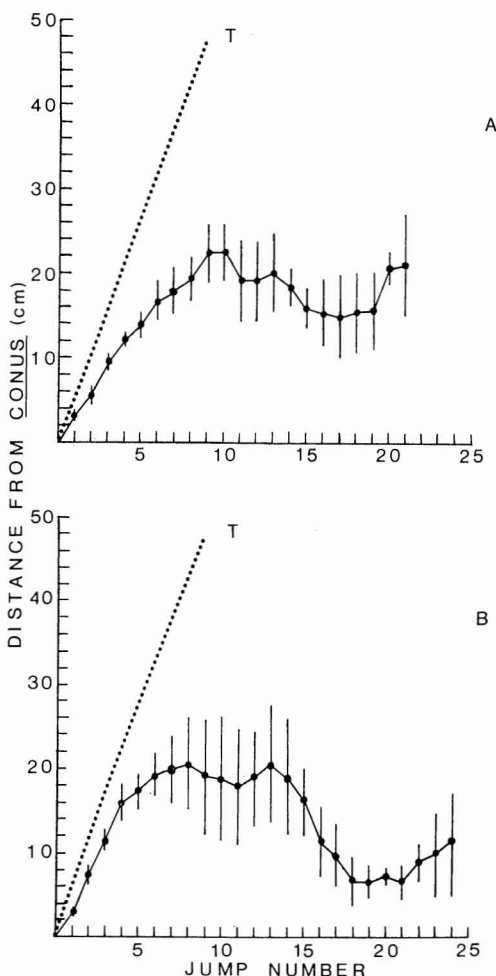


FIGURE 4. Averaged escape paths plotted for the same *Strombus maculatus* as shown in Figure 3. *Conus pennaceus* was present in both experiments. The dotted line, T, indicates the theoretical path of maximum efficiency. A, *S. maculatus* with eyes removed ($N = 6$). B, *S. maculatus* with both eyes and tentacles removed ($N = 6$).

animal was unaffected by this operation ($0.90 < P < 0.95$). No significant effect was produced by the presence or absence of *Conus* in the experimental tray ($0.10 < P < 0.80$, two experiments).

I plotted a theoretical escape response to show the route of most efficient escape, as defined in terms of mean jump distance oriented away from the center along a straight line (Figures 3 and 4). The efficiency of the actual escape can be determined by comparison to this line. I determined mean jump distance crudely

TABLE 1
RESULTS OF ORIENTATION EXPERIMENTS

ANIMAL NUMBER	EXPERIMENT NUMBER	EXPERIMENTAL CONDITIONS	NUMBER OF ESCAPE RESPONSES	NUMBER OF JUMPS*		RATIO
				TOWARD	AWAY FROM	
1	1	<i>Strombus</i> intact; <i>Conus</i> present (Fig. 3A)	9	22	106	0.21
1	2	<i>Strombus</i> intact; <i>Conus</i> absent (Fig. 3B)	7	7	70	0.10
1	3	<i>Strombus</i> blind; <i>Conus</i> present (Fig. 4A)	9	35	74	0.47
1	4	<i>Strombus</i> blind, no tentacles; <i>Conus</i> present (Fig. 4B)	5	38	54	0.70
2	5	<i>Strombus</i> intact; <i>Conus</i> present	4	5	29	0.17
2	6	<i>Strombus</i> intact; <i>Conus</i> absent	4	5	30	0.17
2	7	<i>Strombus</i> blind, no tentacles; <i>Conus</i> present	9	12	78	0.16
3	8	<i>Strombus</i> intact; <i>Conus</i> present	9	12	116	0.10
3	9	<i>Strombus</i> with left eyestalk removed; <i>Conus</i> present	9	34	112	0.30

* "Jumps toward and away from" represent the total number of jumps each *Strombus* made toward or away from the center of the experimental tray during escape responses. "*Conus* present" means the predator remained in the center circle (see Methods) after its contact with the *Strombus*; "*Conus* absent" means the predator was removed following contact.

TABLE 2
COMPARISON OF RESULTS FROM ORIENTATION EXPERIMENTS

CONDITIONS COMPARED	EXPERIMENTS COMPARED	d.f.	χ^2	SIGNIFICANCE
Intact versus Blind	1 versus 3	1	7.177	$0.001 < P < 0.01$
Intact versus Blind and No Tentacles	1 versus 4	1	15.696	$P < 0.001$
	5 versus 7	1	0.009*	$0.90 < P < 0.95$
	8 versus 9	1	9.450	$0.001 < P < 0.01$
Blind versus Blind and No Tentacles	3 versus 4	1	3.503	$0.05 < P < 0.10$
<i>Conus</i> Present versus <i>Conus</i> Absent	1 versus 2	1	1.971*	$0.10 < P < 0.20$
	5 versus 6	1	0.086	$0.70 < P < 0.80$

* Yates' correction.

by dropping a lead shot behind the escaping snail after each jump (for 10 sample jumps) and then by measuring the distance between shots. Jump distance was not affected by eye removal since the ratios (1.8 and 2.0) of mean jump distance:shell length for two blinded animals fell within the range of ratios (1.5–2.5, mean = 1.9) of six intact animals.

DISCUSSION

Although only 12 *Strombus maculatus* were used, a number of interesting aspects of their escape behavior were elucidated.

Nature of the Stimulus

Most gastropod escape responses seem to be caused by a chemical stimulus (Kohn 1961). The effective chemical that elicits the escape response of *S. maculatus* was restricted to those gastropod predators that eat other gastropods (subsequently confirmed by Berg 1974). The only molluscivorous gastropods likely to be encountered by *Strombus* on intertidal limestone benches and subtidal coral reefs in Hawaii are *Conus pennaceus* and *Cymatium nicobaricum*. *Cymatium pileare* and *Conus marmoreus* occur on large sandy areas, subtidal and exclusive of

benches. However, the diet of *C. pennaceus* is not known to include *S. maculatus*, as shown by alimentary tract contents and fecal analysis (Kohn 1959 and personal communication). Kohn has found that *Haminoea simullina* is preferred to *S. maculatus* in choice-chamber experiments (personal communication). Unfortunately, until the food preferences of *Conus* have been studied more thoroughly, the significance of the escape response will remain uncertain.

Attenuation of the Response

The difference in stimulation between live *Conus* and the *Conus* factor is one of intensity; the contact stimulus nearly always surpasses the threshold intensity for eliciting the response whereas the *Conus* factor is much less effective. The results showed a corresponding difference in attenuation of responses to the two stimuli. Is attenuation due to sensory or muscular fatigue or to some central neural process? Although muscular fatigue was probably responsible for the decrease in frequency of jumps toward the end of a response (particularly after an animal had executed 20 or more escapes), habituation by the central nervous system was strongly indicated in experiments in which two stimuli were used—live *Conus* or the *Conus* factor—and then, after attenuation, the needle prod. Muscular fatigue was ruled out because the animal was capable of making subsequent jumps; sensory fatigue was eliminated since the same chemical stimulus caused the response to reoccur after the intervening needle prod (Figure 2A). The chemoreceptors clearly were still functional. When the *Strombus* was placed on a dry surface at the end of the *Conus* factor experiments, it always gave the escape response, demonstrating further that attenuation was not due to inability of the muscles to contract.

Latencies for escape responses have been reported by Feder (unpublished) and Margolin (1964) for gastropod reactions to sea stars. Both investigators found an initial decrease until the fourth trial, when the mollusks showed an increased latency response. This contrasts with the latency periods found in the *Strombus* habituation experiments, where short initial latencies tended to extend over many trials,

slowly increasing and becoming erratic. It is presumed that Margolin's animals habituated, since the final latency before cessation of response was quite long; although he suggested that the results of his first few trials showed a kind of "sensitization," he discussed the matter no further. Habituation in juvenile *S. maculatus* has been shown for the fright reaction that causes withdrawal into the shell (Berg 1972).

Orientation of the Response

The eyes of *Strombus* are among the best developed of those found in gastropods (Charles 1966). Prince (1955) reported that the eyes of the strombid *Pterocera lambis* can converge on an object during visual fixation. It was logical, therefore, to suspect that the eyes might be involved in orientation, although Kohn and Waters (1966) suggested that this might not be so, inasmuch as molluscivorous *Conus* often feed at night. The initial experiments, in which intact *Strombus* were used in the presence and absence of *Conus*, supported this suggestion (see Figure 3A-B). However, blinding the animal caused an increase in its tendency to veer back toward the *Conus* (Figure 4A; see Table 1 for all experiments). Regeneration of strombid eyes has been reported to commence within 24 hr after amputation (Gillary 1971, 1972), and this theoretically could have influenced the results of the blinding experiments. However, the operation did produce a significant effect in orientation (Table 2, discussed below), which tends to negate the above possibility.

These changes in orientation were even more accentuated when the tentacles were removed as well as the eyes. After the first five jumps or so, there was an increase in return and circling jumps (Figure 4B). The following facts were noted: (1) eye removal doubled or tripled (two experiments) the proportion of inward jumps, compared to those made by the intact animal. However, this cannot be attributed to the presence or absence of the *Conus* since the chi-square test shows no significant difference between these two factors (see Table 2); and (2) tentacle removal also caused an increase in inward jumps, although the results were quite variable. The chi-square test indicates that this

operation did not always produce a significant difference in performance between intact and operated animals (Table 2).

The differences between operated and intact animals only became apparent after the first five jumps or so (Figures 3 and 4) because (1) the animal always moves outward on the first jump since it jumps backward, and (2) after a jump, *Strombus* usually lands facing the *Conus*. Therefore, the *Strombus* would be expected to follow a fairly direct path, with or without sense organs, for the initial series of about five jumps. Eyes and tentacles must become important only when the animal needs to maintain a consistent escape course at a distance from the *Conus*. The tentacles should detect the strength of a chemical stimulus; without them the animal cannot tell if it is moving up or down a chemical gradient. Results from animals without tentacles appear to confirm this (e.g., see Figure 4B).

The eyes are not used to see the *Conus* during escape, as was shown by removal of the *Conus* (Figure 3B). Nevertheless, they are important since the blinding experiment produced a significant difference from the control ($0.001 < P < 0.01$, Table 2); it is possible that other visual clues, such as overhead landmarks, the sun, or planes of polarized light are used in orienting the response. Although the escape response movements of operated animals appeared to have been unimpaired, these animals may have experienced side effects that were not directly related to sensory reception.

The similarity of observed slopes to the plotted route of theoretical maximum efficiency (Figure 3A) indicates that the escape response is very efficient in removing *Strombus* from a predator.

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